

## GROWTH DYNAMICS AND THE TAXONOMIC STATUS OF *CLADONIA LEPORINA*

SAMUEL HAMMER

College of General Studies, Boston University,  
871 Commonwealth Avenue, Boston, MA 02215  
e-mail: cladonia@bu.edu

**ABSTRACT.** The unusual gross morphology of *Cladonia leporina* provided the basis for early lichenologists to classify it separately from other species with red apothecia. Their hesitation to include *C. leporina* with other red-fruited species was based on its ascyphose, abundantly branched thallus, which did not match the characteristic cup-shaped morphology of species that were known in the early nineteenth century. *Cladonia leporina* was compared by its author with *C. rangiferina*, which was later recognized within the genus *Cladina*. The concept of a group to accommodate all of the red-fruited taxa in *Cladonia* arose during the nineteenth century. Its morphological parameters were subsequently broadened to include both branched and unbranched species. Contemporary lichenologists have classified *C. leporina* within section *Cocciferae*, in which all of the *Cladonia* species with red apothecia are recognized regardless of morphology. Similar to other branched species with red apothecia, the morphology and morphogenesis of *C. leporina* suggest that this species is allied with taxa outside of section *Cocciferae*.

**Key Words:** *Cladonia*, Cladoniaceae, lichen morphogenesis, meristems, taxonomic history

*Cladonia leporina* Fr. is a locally abundant, endemic lichen in the southeastern United States (Florida to New Jersey) and Cuba. In most modern treatments (Ahti 2000; Evans 1947, 1952; Thomson 1967;) it has been placed within *Cladonia* section *Cocciferae* (Delise) A. Evans on the basis of its red apothecia. In addition to red apothecia (attributable to the presence of rhodocladonic acid), the species that are classified within sect. *Cocciferae* generally possess a persistent primary thallus (basal squamules) and unbranched, cup-forming (scyphose) podetia. However, these characters are lacking in *C. leporina*. As early as the nineteenth century, lichenologists suspected that the highly branched, ascyphose podetium and evanescent primary squamules of *C. leporina* suggested affinities with species outside of sect. *Cocciferae*, possibly outside of *Cladonia* Browne *sensu stricto*. However, most later treatments overlooked the morphological anomalies of *C. leporina* and included it within sect. *Cocciferae* solely on the

basis of apothecial color. At present, sect. *Cocciferae* contains species with a wide range of morphologies that have not been sufficiently documented. The primary objective of this paper is to describe the morphogenesis of the fungal meristem in *C. leporina*. Meristem studies in *Cladonia* are relatively new (see Hammer 2000, 2001a), but they provide insights into patterns of variation and variability in this difficult group of lichen fungi. A second objective is to trace the early taxonomic history of *C. leporina*, with a focus on taxonomic applications that represent conceptual shifts in the approach toward this and other lichen species. The goal is to improve the currently accepted taxonomy in *Cladonia* by presenting biologically relevant information based on morphology and morphogenesis of the fungal meristem. While the micromorphology of this species was not considered by earlier workers, their hesitation to include it within section *Cocciferae* seems to have been an appropriate decision.

#### MATERIALS AND METHODS

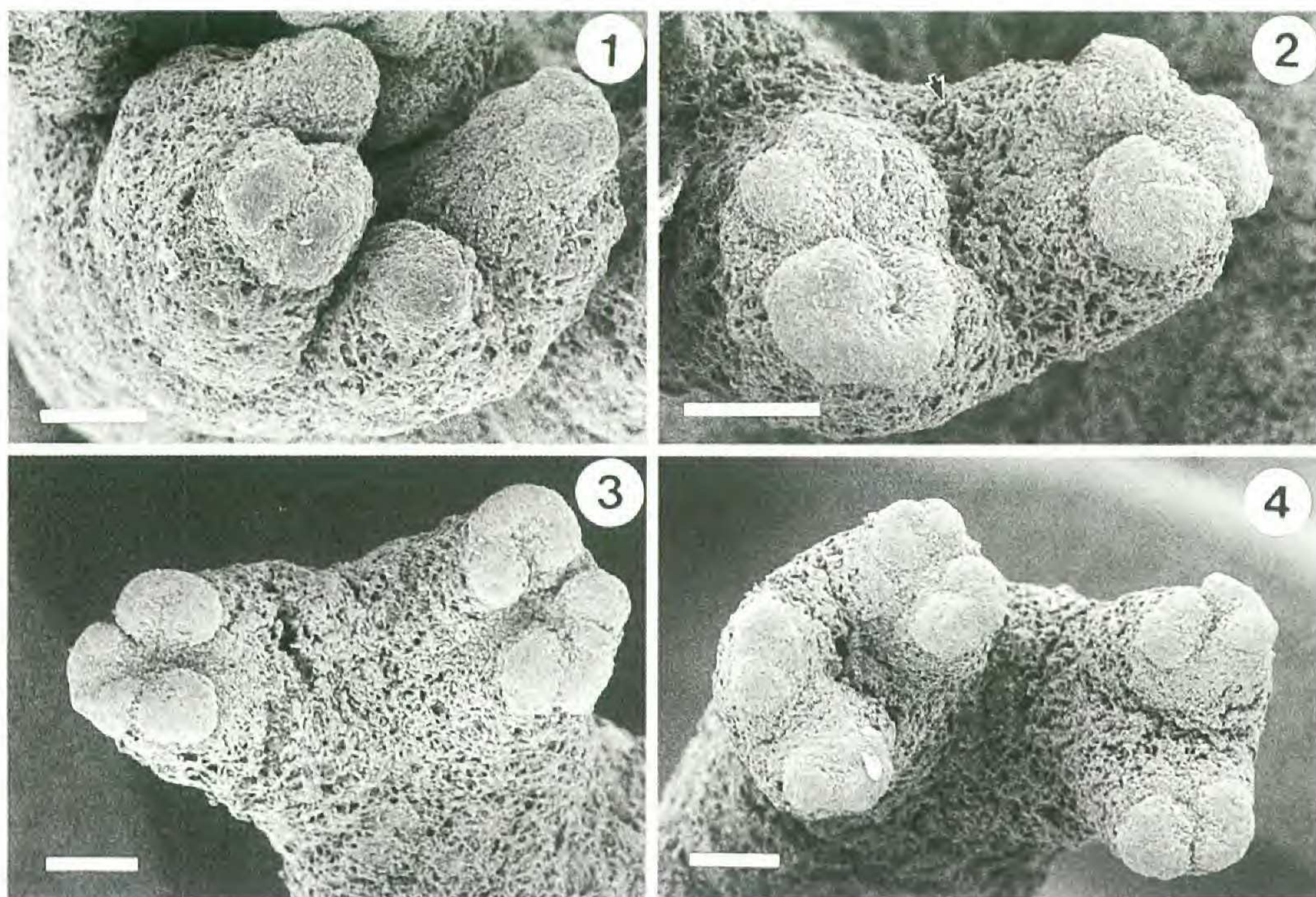
Immature (mostly non-apothecial) specimens of *Cladonia leporina* were studied under the dissecting microscope and were later prepared for scanning electron microscopy (SEM) as described in Hammer (1995, 1996). Scanning electron microscopy was performed at the National Museum of Natural History (Smithsonian Institution) on a Phillips 501 electron microscope at 10–20 kv. Table 1 provides a list of selected specimens studied. A note on the terminology used in this paper seems appropriate. The term “meristem,” which is usually applied to plants (see Barlow 1989) is used in a broad sense in this paper (see Hammer 2000, 2001a). It refers to the purely fungal tissue system that is usually (but not exclusively) found near the apices of *Cladonia* lichens. It is called a meristem because it gives rise to the rest of the hyphal cells of the podetium (see Hammer 1993). Similarly, the term “branch” is most appropriately applied to plant form (see Bell 1991). It has also been used to describe lichen growth, particularly the narrow, elongate structures that arise laterally or apically from the erect, secondary thallus (podetium) in *Cladonia* (see Hammer 1997b).

Table 1. Representative specimens of *Cladonia leporina* examined for this study.

Specimen	Locality
<i>Tucker 10118</i> (FH)	Alabama
<i>Evans 650</i> (FH)	Florida
<i>Hammer 7733</i> (FH)	Florida
<i>Hammer 7750</i> (FH)	Florida
<i>Rapp 15</i> (FH)	Florida
<i>Thaxter 158</i> (FH)	Florida
<i>Small s.n.</i> (coll. 1894) (FH)	Georgia
<i>Seymour &amp; Earle 9195</i> (FH)	Mississippi
<i>Evans 214</i> (FH)	North Carolina
<i>Ravanel s.n.</i> (FH)	South Carolina
<i>Parks 21259</i> (FH)	Texas
<i>Luttrell 1904</i> (FH)	Virginia
<i>Imshaug 25324</i> (FH)	CUBA
<i>Wright s.n.</i> (FH-TUCK)	CUBA

RESULTS

The podetia of *Cladonia leporina* are abundantly branched, but in general the branches are initiated closer to the base than in species such as *C. furcata* (Huds.) Schrad. or *C. crispata* (Ach.) Flot. Further, the branches of *C. leporina* lack the axial openings that characterize most other branched species in the Cladoniaceae. Branching in *C. leporina* can be traced to the ontogeny of the fungal apical meristem. In particular, the initial patterns of meristem splitting are reflected in later branching morphology. The meristem, which initiates and controls growth in *C. leporina*, splits early and frequently during ontogeny. The indeterminate number of branches at maturity and their varied orientation reflects early variations in filial meristems. The asynchronous development of separate meristems and torsion of the axis of growth leads to further variability at maturity. Meristem splitting and subsequent branching of the lichenized thallus is dichotomous but not necessarily equal (Figures 1–4). After the meristem splits, certain bundles develop faster than their filials, enlarging and splitting before same-age bundles have developed apace (see meristems labelled c and c' in Figure 5). In general, the meristem splits dichotomously. However, the angle of divergence varies among filial meristems and this tends to increase during ontogeny. For example, the initial meristem splits occur at relatively small



Figures 1–4. Early ontogeny of *Cladonia leporina* (SEM). 1. Dichotomous branching with limited meristem splitting. The left-hand branch system (two meristems) shows an enlarging meristem below. 2. Two developing branch systems from an initial split (arrow). Right-hand branch system (three meristems) is further developed than the left-hand branch system, which is incompletely split into two bundles. 3. Two well developed branch systems separated by lichenized tissue (note loose network of surface hyphae). 4. Advanced meristem growth with several meristems on two branches. Note that the meristems have split at various angles. All scale bars = 100  $\mu\text{m}$ .

angles (Figures 1, 5), which increase during later growth (Figures 4, 5). As a result, the axis along which splitting occurs and the orientation of filial bundles differ. In addition, torsion of the meristem occurs, leading to variable branch orientation later in ontogeny (Figures 2–4). Further, a group of more or less same-age branches may develop at various rates, resulting in the apparent deformation of a roughly circular or ovoid grouping of meristem bundles (Figures 6–9). The development of a roughly ovoid apical cluster is often accompanied by the exaggerated development of lichenized tissue below. In general, the meristems split and develop slowly, while the tissue beneath them develops relatively quickly. The result is an urn-like podetial shape that is narrow at the apex and wider below (Figure 6). The meristem eventually separates during ontogeny as the branches become longer (Figure 7), but the process of separating may be delayed so that branching

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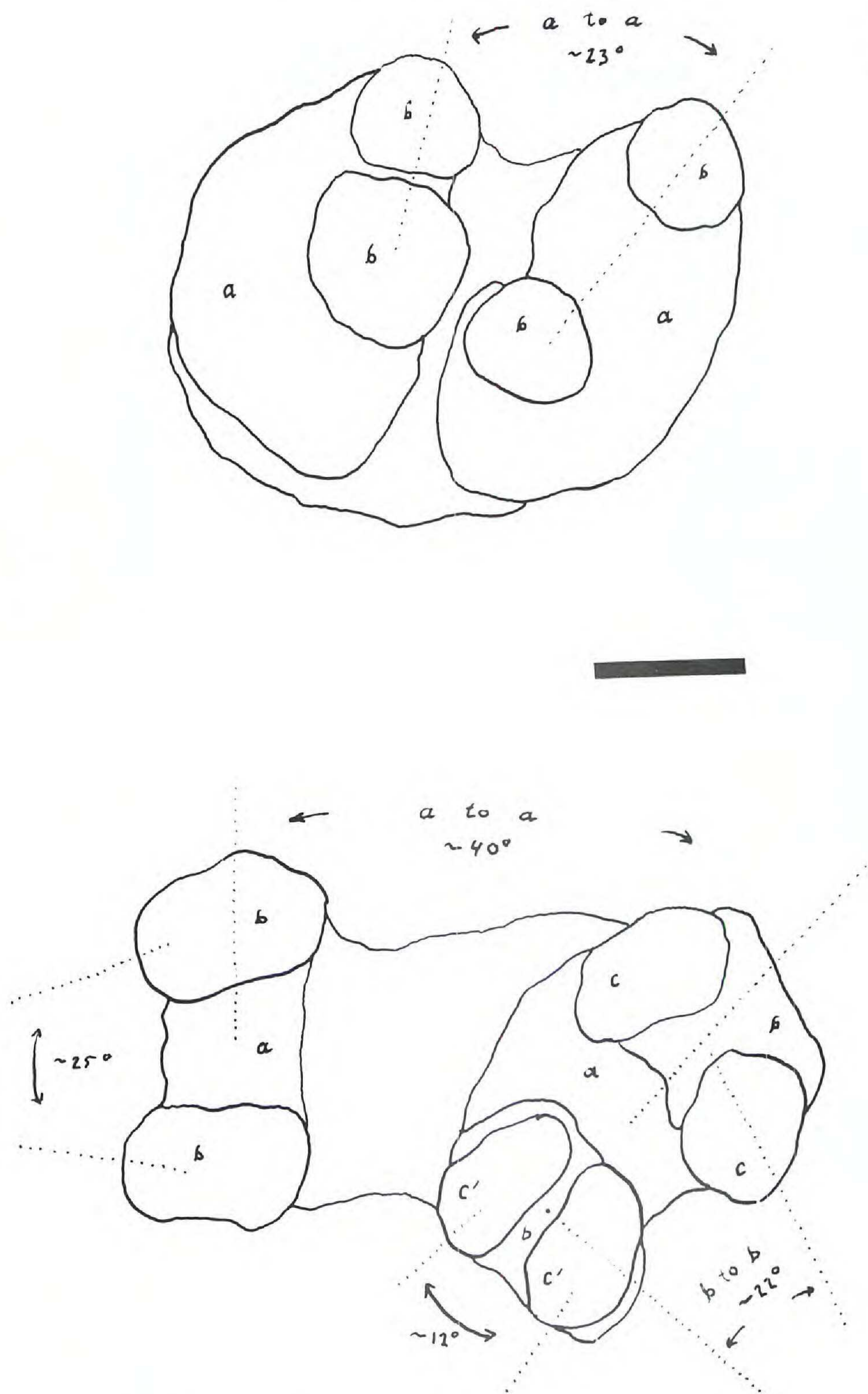
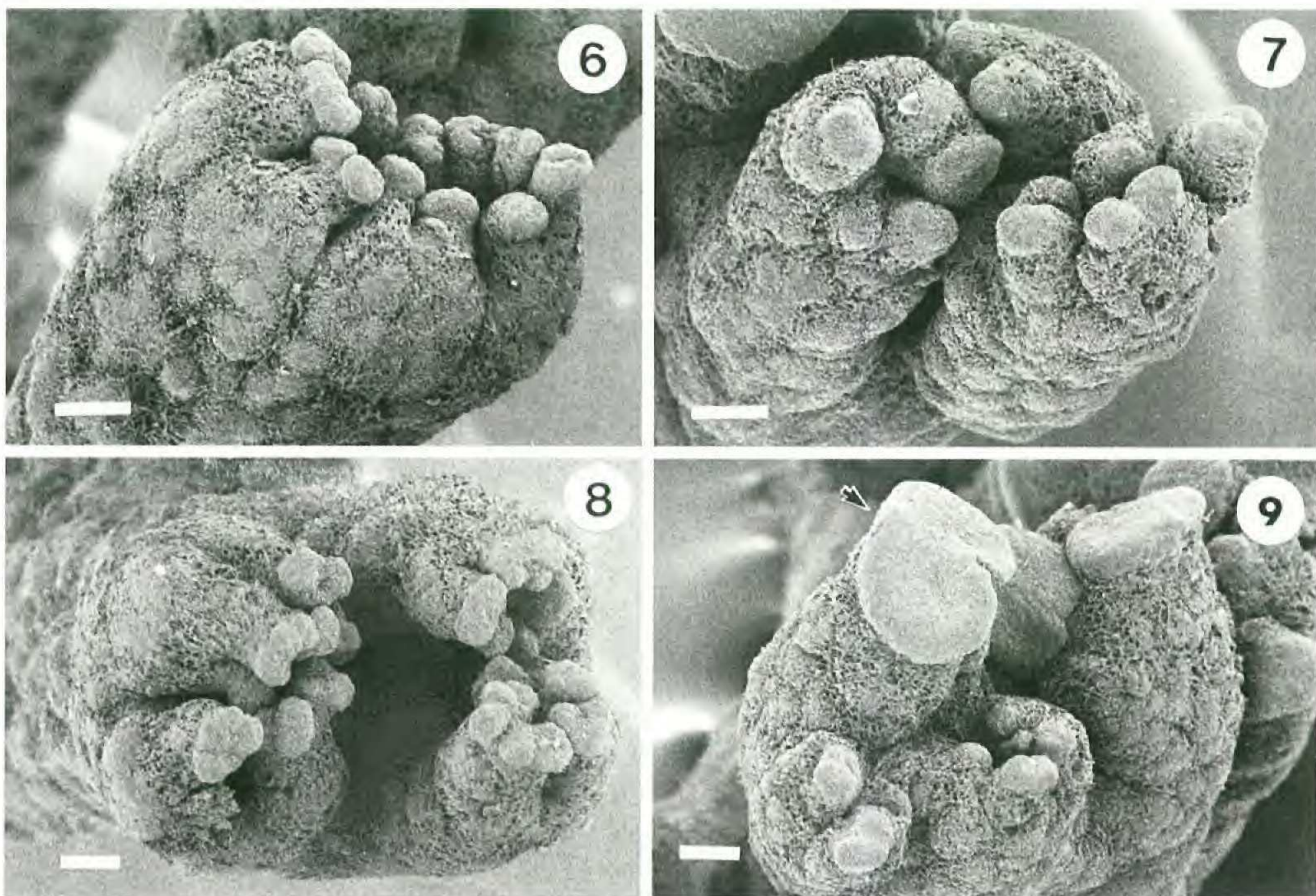


Figure 5. Diagrams based on SEM photographs of *Cladonia leporina* illustrating approximate angles of meristem divergence among filials. Note that the angle of divergence increases between older meristem filials. ("a" indicates oldest filials). Scale bar ca. 100  $\mu\text{m}$ .



Figures 6–9. Later meristem development in *Cladonia leporina*. 6. Portion of developing podetial apex. Meristems have split but remain clustered around a central axis. 7. Later apical development with more or less same-age (filial) branches with meristems at various stages of development. 8. Further meristem splitting at podetial apex. Note underlying axis (lichen tissue) and thick bases of developing branches. 9. Developing apothecium (arrow) adjacent to immature branches that are tipped by meristem tissue (below). All scale bars = 100  $\mu\text{m}$ .

in certain parts of mature podetia is indistinct (Figure 8), especially when observed macroscopically. In some podetia, the difference in rates of meristem development is highly pronounced, and apothecia may develop on branches that are roughly the same age as branches that are tipped by the immature meristem (Figure 9).

#### DISCUSSION

The branching ontogeny of *Cladonia leporina* occurs through various processes. Enlarging and splitting meristems are the major factors that influence morphogenesis of the branched lichenized podetium, but other factors control the development of branches as well. For example, torsion and synchronization influence the outcome of form in *C. leporina*. In addition, the growth and development of lichenized tissue immediately below the

branches affects branching patterns and morphogenesis in this species, similar to the pattern seen in the Australasian endemic *C. pertriosa* Kremp. (see Hammer 2001b). *Cladonia leporina* is characterized by branching, but cup-like or urn-like growths are also present in this species. However, the development of cups does not occur as described in Hammer (1993, 2000). Instead of the cup forming from a single meristem that undergoes various growth processes, the cup-like form of *C. leporina* is a by-product of relatively slow meristem splitting accompanied by the growth of more massive supporting lichenized tissue. The cup-like shape may be maintained by the mechanical force of the tissue beneath the meristem, in contrast to other species in which the shape of the cup is determined by the outward growth of a single toroidal (donut-shaped) meristem. Thus, the cup of *C. leporina* is the product of a developmental pathway that is distinct from other *Cladonia* species. The cup in *C. leporina* is analogous, not homologous to cups in other *Cladonia* species. Thus *C. leporina*, as described by early workers, is ascyphose when the morphogenesis of its cups is compared to that of other *Cladonia* species.

Historically, the unusual morphology of *Cladonia leporina* was considered more important than its apothecial color in the taxonomic placement of the species. When the species was first described by Fries (1831), it was not classified among red-fruited taxa, in which all the known species possessed cups. Fries was equivocal about the placement of *C. leporina* and he compared its morphology to *Cladonia* (= *Cladina*) *rangiferina* (L.) Nyl., a branched species with brown apothecia. However, Fries stressed the red apothecia (“apotheciis coccineis distinctissima”) of *C. leporina* and he understood that they required some sort of taxonomic distinction. Fries sought a solution to the problem of *C. leporina* within another morphological parameter based on the characteristics of the primary thallus. His taxonomic system recognized two sections in *Cladonia* based upon the primary thallus and its morphology. Section I was characterized by a leaf-like (squamulose) primary thallus. He included four series within this section based on apothecial color. However, he did not place *C. leporina* within the so-called Series IV (*Cocciferae*), with the other red-fruited species. Rather, he placed *C. leporina* in an ambiguous position between his species number 210 (*C. macilenta* Hoffm.), which was the last species in Section I, and species number 211 (*C. rangiferina*), the first of three species in Section

II, which was characterized by a crustose primary thallus. Fries added to the ambiguous position of *C. leporina* by including its description in the paragraph that introduced Section II, but he did not assign it a species number!

The diagnosis of *Cladonia leporina*—"Thallus horizontalis crustaceo-granulosa, granulis in podetia abeuntibus. Podetia uniformia, fruticulosa, ascypha, definite ramosa"—was included in Fries' description of his Section II, which he referred to the group *Pycnothele* of Acharius (1803). The three species in Section II, *C. rangiferina*, *C. uncialis* (L.) Wiggers, and *C. papillaria* (= *Pycnothelia papillaria* Dufour) were placed together on the basis of their crustose primary thallus. Thus in the case of *C. leporina*, Fries followed the tradition that was begun by Acharius, who classified the species by morphology instead of apothecial color. Flörke (1828) had also followed this tradition. For example, three years before *C. leporina* was described, he placed the red-fruited *C. incrassata* Flörke in the group *Clavatae* with species of similar morphologies and various apothecial colors. While Acharius, Flörke, and Fries did not ignore the color of the apothecium, it did not take precedence over morphology in their systems.

By contrast, Delise (in Duby 1830) used color as a major taxonomic character. He erected the *Cocciferae* grouping within the genus *Cenomyce* (= *Cladonia*) to accommodate all of the species with red apothecia together, irrespective of morphology. Nylander (1858) adopted Delise's approach, with a stress on color as the deciding factor in the classification of many of the species of *Cladonia*. Tuckerman (1882) also based his classification of *Cladonia* upon the color of the apothecia. However, he struggled to accommodate the unusual morphology of *C. leporina* within his system. Tuckerman recognized three series in *Cladonia*. He included *C. leporina* as the last species (number 31) in Series III (*Coccineae*) taking care to compare its morphology to brown-fruited species in Series I (*Fuscae*). By referring to the group *Fuscae*, Tuckerman compared *C. leporina* to varieties of the branched species *C. furcata*, including var. *crispata* (= *C. crispata*). Tuckerman also mentioned the similarity between *C. leporina* and *C. rangiferina* that Fries had observed. The monographer Vainio (1887) listed *C. leporina* as the last species (his number 36) in the *Cocciferae*, following *C. cristatella* Tuck. In Vainio's taxonomy (it is noteworthy that he considered it to be a phylogenetic arrangement), the species that followed *C. leporina*

was the brown-fruited *C. aggregata* [= *Cladia aggregata* (Sw.) Nyl.]. Like Fries, Vainio held an equivocal view of the placement of *C. leporina*. He described it as “ascypha,” which reflects the gross morphology of the highly branched podetium, but he included it marginally within the *Cocciferae*.

Evans (1947, 1952) considered *Cladonia leporina* in several papers. He compared its morphology to species in the genus *Cladina* as well as to *Cladonia uncialis*, a brown-fruited species with characteristically perforate branch axils (largely absent in *C. leporina*). While Evans placed *C. leporina* in the *Cocciferae*, he proposed a new monotypic taxon (series *Leporinae*) to accommodate its morphology (Evans 1938). *Leporinae* was unique in that it was based on morphological characters while the other groupings within *Cocciferae* were based solely upon color differences in the species. Thomson (1967) later included *C. leporina* as the final species in the *Cocciferae* but did not provide a particular heading for it or any of the other red-fruited *Cladonia* species. Ahti (2000) included *C. leporina* as one of 38 (alphabetically arranged) *Cocciferae* species in the neotropics. The group delimited by Ahti shows a very wide range of morphological characters. Many of the species are new to science and require further morphological study.

If *Cladonia leporina* is to be included in sect. *Cocciferae* along with other branched, red-fruited species such as *C. cristatella* (see Hammer 1997c), *C. incrassata* (Hammer 1997a), or the recently described *C. piedadensis* Ahti (see Ahti 2000), then we may assume a very broad range of morphologies within the group, which has traditionally been circumscribed upon the basis of apothecial color alone. Contemporary lichenologists have classified *C. leporina* within sect. *Cocciferae*, in which all of the *Cladonia* species with red apothecia are recognized regardless of morphology. The underlying assumption of this classification system is that taxonomically, chemistry and color are more important than morphology in *Cladonia*. From a phylogenetic standpoint, this would imply that the production of rhodocladonic acid, which results in red apothecia, arose once in *Cladonia* and probably denotes a monophyletic group. Following this assumption, morphological or morphogenetic characters would perforce represent multiple evolutionary events. That certain morphologies arose a number of times is a scenario that is difficult to accept given the apparently tight controls on early morphogenesis in the Cladoniaceae.

(see Hammer 2001a). Further hypotheses about monophyly among *Cladonia* species have yet to be tested, but so few taxa have been analyzed morphologically that pertinent information is still lacking. Preliminary molecular data (see Stenroos and DePriest 1998) support the hypothesis that the species in sect. *Cocciferae* are related, but most of the species in the group have not yet been studied. Perhaps more important, the genetic basis for the production of rhodocladonic acid is unknown. Does it represent an autapomorphy that characterizes sect. *Cocciferae*? Alternatively, might sect. *Cocciferae* be more a product of the cognitive biases of taxonomists than biology? In other words, has the ease with which red apothecia are recognized contributed to the taxonomic decision to classify the red-fruited species together? Most significantly, what are the genetic controls over morphogenesis in *Cladonia* fungi? In order to better evaluate the taxonomy of sect. *Cocciferae* and the Cladoniaceae in general, future projects should undertake to examine the inherited pathways by which form and color are attained. This may help to improve the state of our knowledge concerning the origin and relationships of the Cladoniaceae, which is still quite vague. Until then, two considerations might be applied to the taxonomy of *Cladonia*, with the goal of constructing more biologically relevant groupings within the genus. From a narrow perspective, *C. leporina* should be classified apart from the *Cocciferae*. More broadly, rather than struggle to classify *C. leporina* in a similarly arbitrary grouping, the problems of its taxonomy should serve as a focal point for reconsidering all of the subgeneric taxa in *Cladonia*.

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#### LITERATURE CITED

- ACHARIUS, E. 1803. *Methodus Lichenum*. Ulrich, Stockholm, Sweden.  
AHTI, T. 2000. *Flora Neotropica Monograph 78: Cladoniaceae*. The New York Botanical Garden Press, Bronx, NY.

- BARLOW, P. W. 1989. Meristems, metamers, and modules and the development of shoot and root systems. *Bot. J. Linn. Soc.* 100: 255–279.
- BELL, A. D. 1991. *Plant Form*. Oxford Univ. Press, Oxford, UK.
- DUBY, J. E. 1830. *Botanicon Gallicum (Pars Secunda)*. Bouchard- Huzard, Paris, France.
- EVANS, A. W. 1938. The *Cladoniae* of New Jersey—supplement. *Torreyia* 38: 137–149.
- . 1947. A study of certain North American *Cladoniae*. *Bryologist* 50: 14–54.
- . 1952. The *Cladoniae* of Florida. *Trans. Connecticut Acad. Arts* 38: 249–336.
- FLÖRKE, H. G. 1828. *De Cladoniis difficillimo Lichenum genere commentatio nova*. Rostock, Germany.
- FRIES, E. 1831. *Lichenographia Europaea Reformata*. Berling, Lund, Sweden.
- HAMMER, S. 1993. Development in *Cladonia ochrochlora*. *Mycologia* 85: 84–92.
- . 1995. Primary tissue and the structure of the podetium in *Cladonia*. *Mycologia* 87: 46–53.
- . 1996. Variation and variability in *Cladonia* section *Perviae*. *Mycologia* 88: 71–79.
- . 1997a. Branch initiation in the lichen *Cladonia cristatella* (British Soldiers). *Rhodora* 99: 23–32.
- . 1997b. Branching dynamics in *Cladonia subtenuis*. *Mycologia* 89: 461–467.
- . 1997c. The unusual deflexed podetium of the lichen *Cladonia incrassata*. *Rhodora* 99: 287–301.
- . 2000. Meristem growth dynamics and branching patterns in the Cladoniaceae. *Amer. J. Bot.* 87: 33–47.
- . 2001a. Lateral growth patterns in the Cladoniaceae. *Amer. J. Bot.* 88: 788–796.
- . 2001b. Variability and ontogenetic process in *Cladonia pertriosa*. *Australas. Lichenol.* 48: 10–15.
- Nylander, W. 1858. *Synopsis Lichenum*. Martinet, Paris, France.
- STENROOS, S. AND P. DEPRIEST. 1998. SSU rDNA phylogeny of cladoniiform lichens. *Amer. J. Bot.* 85: 1548–1559.
- THOMSON, J. W. 1967. *The Lichen Genus Cladonia in North America*. Univ. Toronto Press, Toronto, Canada.
- TUCKERMAN, E. 1882. *Synopsis of the North American Lichens*. Cassino, Boston, MA.
- VAINIO, E. 1887. *Monographia Cladoniarum universalis*. *Acta Soc. Fauna Fl. Fenn.* 4: 1–510.